

Studies on the collembolan populations of several plant communities of the Basque Country (Spain)

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Synopsis: The structure and composition of Collembola in three forests (beech, oak and pine) and in a meadow have been studied. Seasonal changes in diversity and vertical distribution of species have been detected, being the water content and important edaphic factor that affects the populations.

Keywords: Collembola, plant communities, litter, soil, edaphic factors, diversity, vertical distribution.

INTRODUCTION

By the diversity of media that species inhabit and by their responses to the environmental variations, Collembola is a group of microarthropods which have been the subject of many ecological studies for the last years. If the existence of an indirect relationship between plant and soil arthropod communities (USHER *et al.*, 1982) is accepted, it seems evident that different soils (directly influenced by vegetation) must support collembola communities which will differ not only with regard to specific composition but also with regard to hierarchical structure.

Though it exists an abundant literature on collembola communities in temperate areas, no many comparative studies have been undertaken to show both seasonal and structural variations of the collembolan populations in different plant communities simultaneously. This is particularly true in

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Spain, where no ecological surveys about collembola existed before the studies of SELGA (1966), who followed the pattern of CASSAGNAU (1961) in France.

The Basque Country is a geographical region where little is known about this animal group. So that, in the last years, we have been interested in the knowledge of collembola of this region with the aim of showing ecological aspects not only intrinsic to the populations, but also to the relationship with the physical environment.

This work follows some initiate studies (POZO & MARTINEZ, 1983). Here, we refer to the composition, structure, diversity, vertical distribution and seasonal changes of the collembola populations in soils of four different plant communities. Later, one of us (POZO, preparing), will refer to the environmental factors that seem to affect the species distribution, by mean of multivariate analysis.

I. — STUDY SITES

The study sites were chosen so that the most significant plant communities of the Basque Country were present, as well as the road-way system allows to sample all the sites in the same day. They are the following:

1. Beech forest. *Fagus silvatica* L. U.T.M.: 30TWN079618. 400-500 metres above sea level.
2. Oak forest. *Quercus robur* L. U.T.M.: 30TWN108590. 550 metres above sea level.
3. Mixed pine forest of *Pinus silvestris* L and *Pinus pinaster* (Soland). U.T.M.: 30TWN197572. 650 metres above sea level.
4. Meadow. U.T.M.: 30TVN868864. 250 metres above sea level.

The geological substratum of these systems is mainly composed of marl and sandstone, with a limestone component in the case of the pinewood, belonging to the cretaciuous-age, which has given rise to forest brown soils.

The studied areas are located in a region of a relative climatic uniformity, so that there are not big differences among them, neither on the rainfall nor on the temperatures, as show the rainfall-temperature diagrams following GAUSSEN (1955) in figure 1. All the

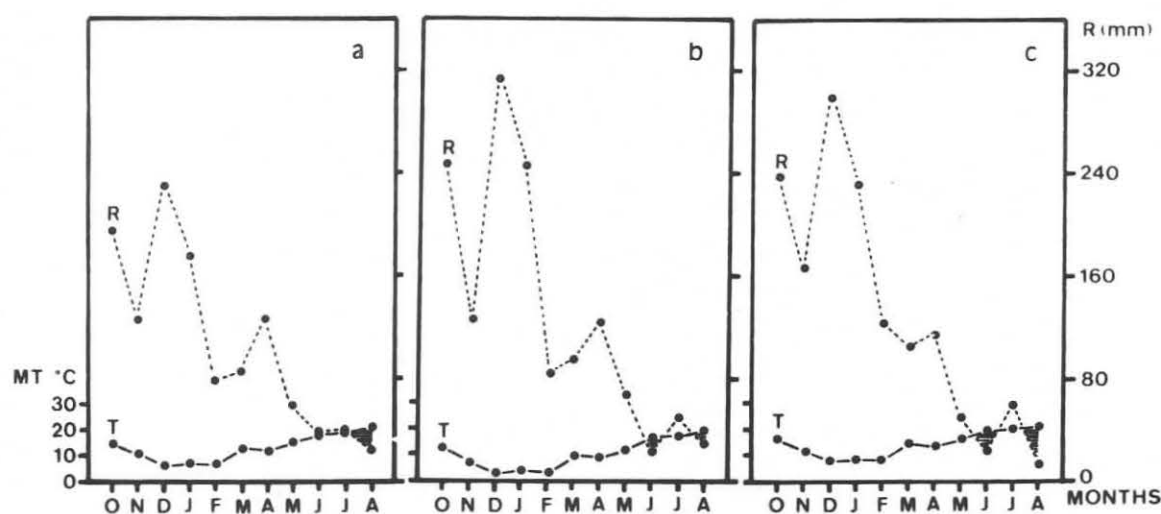


FIG. 1. — Monthly rainfall (R) and mean temperature (MT) changes. October 1980-August 1981.
a, beech and oak forests; b, pine forest; c, meadow.

sites are characterized by heavy rainfall in autumn and winter, with moderate temperatures during the whole year. It is possible to remark light dryness conditions in summer, when the values of the temperature overcome those of the rainfall (Fig. 1).

II. — MATERIAL AND METHODS

Samples were taken seasonally in November 1980 and February, May and August 1981. Every month 6 samples of litter and 6 of soil (0.5 cm depth) of about 250 cc were collected in each area.

The number of samples examined amounts to 192. Parallel were taken for chemical analysis.

The extraction of collembola was made by using Berlese-Tullgren funnels.

The edaphic parameters measured were: water content of the samples by drying at 105° C; temperature in the surface of the litter as well as at about 3 cm depth in the soil; pH, according to the method of the International Society of Soil Science, in distilled water as well as in 1N KCl; organic carbon from samples sieved to 0.5 mm and dried at 105° C, by oxidation with $K_2Cr_2O_7$ and titration with Mohr salt; nitrogen according to the Kjeldahl method. The two last parameters allow us to determine the C/N ratio, a basic index of the biological activity.

As an information about the number of species of collembola and their relative abundances within a community, diversity was measured by using the Shannon-Weaver index (MARGALEF, 1974):

$$\begin{aligned}
 H &= -\sum p_i \log_2 p_i & H &= \text{species diversity} \\
 H_{\max} &= \log_2 a & H_{\max} &= \text{maximum diversity (species richness)} \\
 E &= \frac{H}{H_{\max}} & p_i &= \text{probability of species « i »} \\
 & & a &= \text{number of species} \\
 & & E &= \text{evenness}
 \end{aligned}$$

III. — RESULTS AND DISCUSSION

A) Climatic and edaphic factors.

As a consequence of the climatic conditions the different soils have moisture saturation during November, February and May as the average value of the water content is above 20 % (AGRELL, 1941). This is shown in figure 2.

The litter of different types of forest keep similar moisture level in November, February and May and suffers an important decrease in summer. That is not observed in the meadow, which in summer keeps similar hydric conditions to the previous seasons because the most part is not true litter, but living matter.

The results of the temperature, measured in litter and soil (Fig. 3), show a different dynamics from the water content, influencing doubtless the values of the latter parameter. This temperature values are punctual data of sampling that does not show neither the daily variations nor quite climatic differences among the areas, due to the elapsed time in sampling among the sites. Nevertheless, we can speak about differences between the two layers of each area. In the three ecological systems where a well defined litter

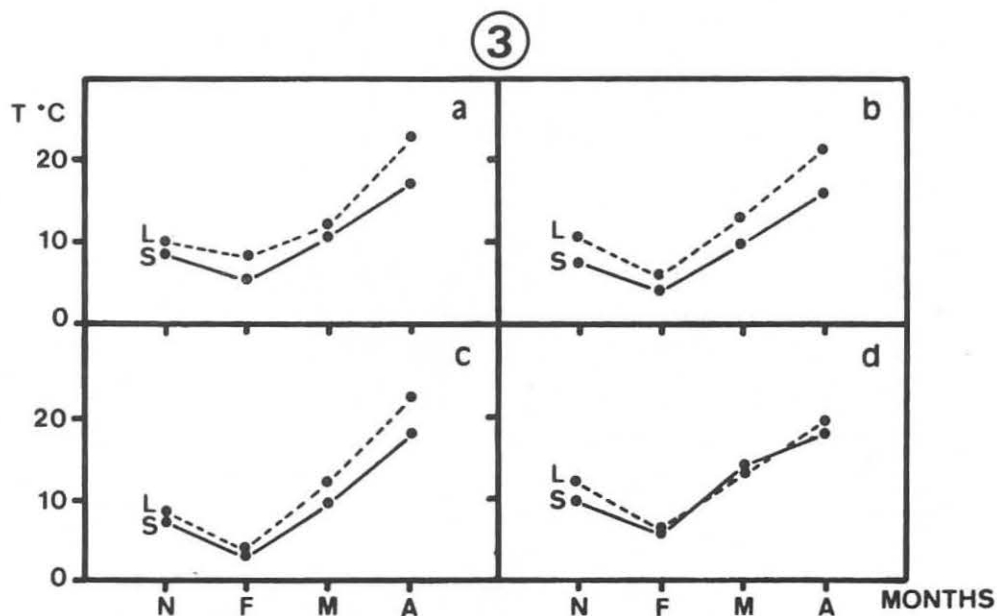
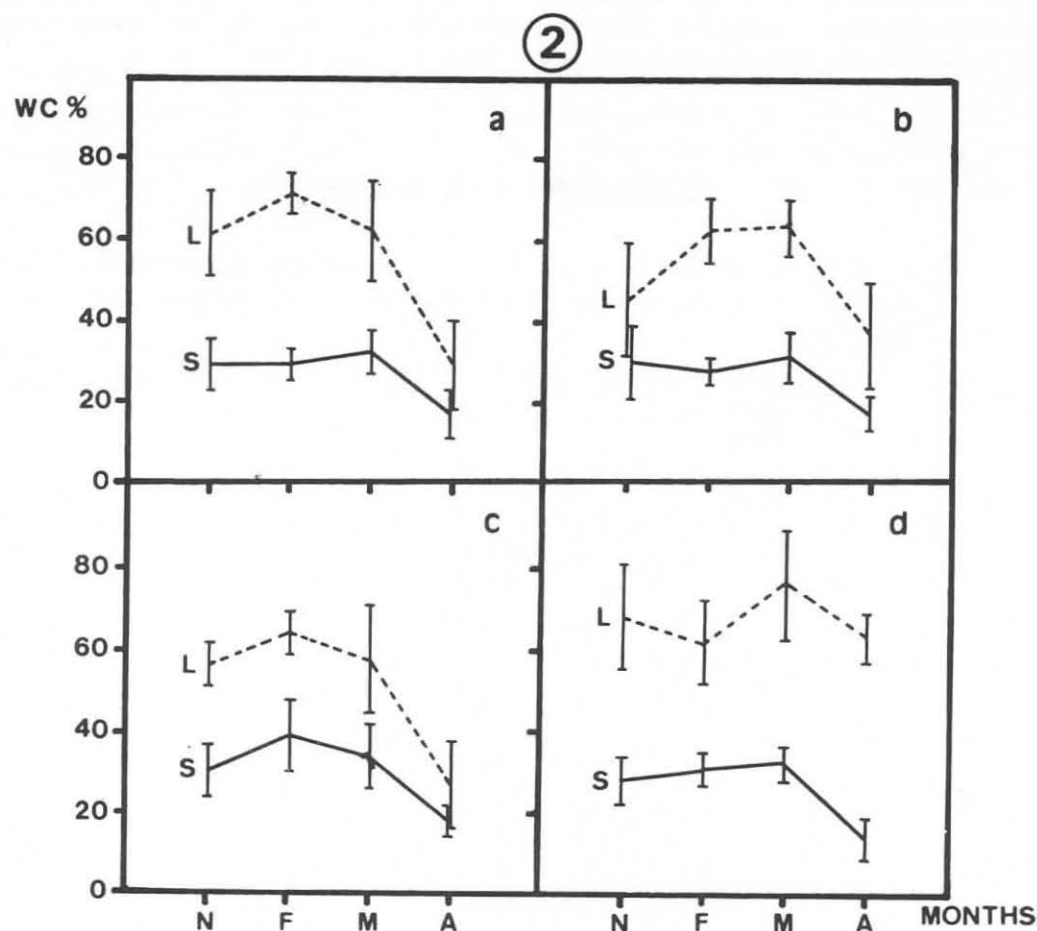


FIG. 2. — Seasonal changes in the water content (WC) of litter (L) and soil (S). a, beech forest; b, oak forest; c, pine forest; d, meadow. N = November; F = February; M = May; A = August. $\bar{x} \pm t$ SE, $n = 6$.

FIG. 3. — Seasonal changes in the temperature values in litter (L) and soil (S). a, beech forest; b, oak forest; c, pine forest; d, meadow. N = November; F = February; M = May; A = August.

layer exists (forests), the soil temperature values always are below those registered at litter surface, with big differences in summer. It is in this season when we could speak of a protective effect of the litter towards the soil. In the other hand, in meadow, where no vegetal cover exists, therefore isolation is greater, and no well defined litter layer is developed the difference between surface (living matter) and soil are smaller.

The composition of vegetation of an area has an important effect on the soil nature and the humus type. It is evident that there are differences among organic deposits of conifers, deciduous trees and meadows, not only qualitatives but also quantitatives. In this regard, NOIRFALISE and VANESSE (1975) indicate that the accumulation of organic matter is larger in soils planted with *Pinus silvestris* than in beechwoods and much greater than in oakwoods. This fact has also observed in this study (Tab. I). The percentage of organic matter in the pine forest soil is significantly larger than in the other sites (one way analysis of variance, $F = 41.38$, $p < 0.01$; t-test value between the pine forest and the beech forest, that is the nearest value, is 2.83, $p < 0.01$).

TAB. I

Edaphic chemical parameters of soil samples (0-5 cm depth) of studied sites. $\bar{x} \pm t$ SE

	Organic Matter (%)	C (%)	N (%)	C/N	pH H ₂ O	pH ClK
Beech forest.....	7.47 \pm 1.19	4.33 \pm 0.69	0.26 \pm 0.07	18.56 \pm 4.72	4.78 \pm 0.13	3.73 \pm 0.15
Oak forest.....	5.23 \pm 0.53	3.03 \pm 0.31	0.15 \pm 0.06	23.58 \pm 11.48	5.12 \pm 0.21	4.19 \pm 0.21
Pine forest.....	13.26 \pm 1.79	7.70 \pm 1.04	0.26 \pm 0.09	29.56 \pm 7.27	5.08 \pm 0.22	4.17 \pm 0.22
Meadow.....	6.51 \pm 0.61	3.65 \pm 0.56	0.25 \pm 0.11	18.36 \pm 8.78	5.37 \pm 0.22	4.24 \pm 0.25

On the other hand, results obtained concerning the pH allow to distinguish the different kinds of soils according to the acidity. Thus, the meadow has higher pH, whereas the beechwood is the most acid. Or, in other words, the pH of the beechwood soil shows a significant difference with any other soil (one way anova, $F = 6.55$, $p < 0.01$; t-test value between the beech forest and the pine forest, that has the nearest mean value, is 2.24, $p < 0.05$).

Differences among the C/N ratios can be explained on the basis of the different composition of the vegetation (GARAY, 1980). It seems that the soils of the coniferous stands present a higher C/N ratio than the soils of the deciduous woods. It is true if we accept that the C/N values decrease as speed of litter decomposition increases (WITTICH, 1943). The results of this study have revealed that the averages of the C/N ratio of the pine forest soil are higher than those of the beech forest and the meadow (U-test significative, $p < 0.05$). The values of the C/N ratio of the oak forest soil, although not statistically different from the other sites, show that in some situations the higher values will be due to a greater nitrogen deficiency than in the other soils (Tab. I).

B) Collembola populations.

1. General Structure.

The number of individuals of each species in each of the studied sites and layers is summarized in table II. The total number of collembola is 12,067. Oakwood and pinewood show the higher values of abundance, followed by meadow and beechwood. It seems that sites with higher C/N ratios, pine forest and oak forest, show bigger numbers of collembola than sites with lower C/N ratios, beech forest and meadow. With regard to the distribution by layers of these global populations, in the deciduous woods the higher proportion of individuals corresponds to the soil, whereas in the pine forest, the litter has the larger population. The meadow has similar proportions in the herbaceous layer and in the soil.

Although we cannot speak of a true population dynamics, because it would be necessary to sample in a more frequent way, we can look to the differences in abundance of collembola in the different seasons. Figure 4 shows the seasonal variations. Excepting the winter in the oakwood, it can be said that collembola in both litter and soil, in a particular area, have similar trends. Reductions in abundance in summer, especially referring to the litter layer, may be pointed out. Without doubt, this fact is caused by drying of the litter, preventing the normal development of collembola, and

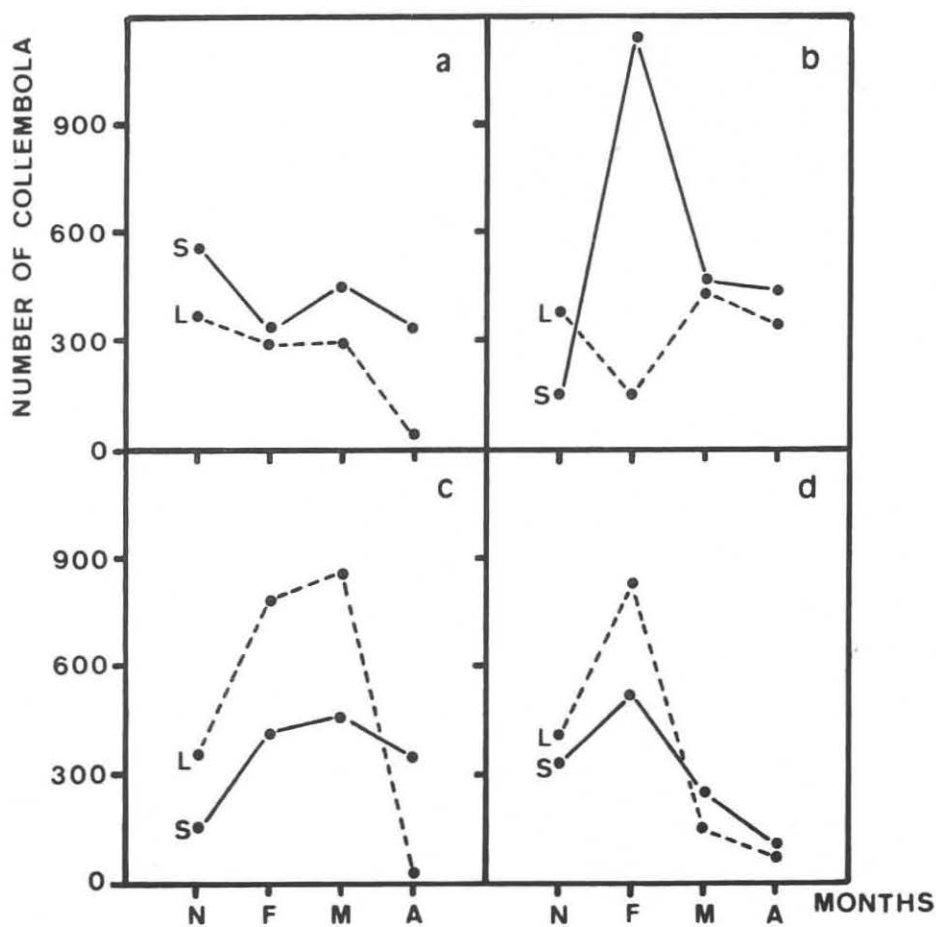


FIG. 4. — Seasonal changes in total abundances of Collembola. L = Litter; S = Soil. a, beech forest; b, oak forest; c, pine forest; d, meadow. N = November; F = February; M = May; A = August.

TAB. II

Total abundances of the Collembola species in litter (L) and soil (S) of the studied sites

Species	Beech Forest		Oak Forest		Pine Forest		Meadow	
	L	S	L	S	L	S	L	S
<i>Hypogastrura meridionalis</i> Steiner.....	7	—	—	—	22	68	—	—
<i>Hypogastrura hispanica</i> Steiner.....	—	—	—	—	—	28	—	—
<i>Ceratophysella armata</i> (Nicolet).....	10	6	1	6	205	185	1	3
<i>Ceratophysella attenuata</i> Cassagnau....	49	15	2	2	1?	—	—	—
<i>Xenylla grisea</i> Axelson.....	2	—	89	—	—	—	5	—
<i>Xenylla tullbergi</i> Börner.....	4	—	—	—	—	—	—	—
<i>Willemia anophthalma</i> Börner.....	10	13	—	—	—	—	—	—
<i>Willemia aspinata</i> Stach.....	6	—	—	—	—	14	—	—
<i>Friezea truncata</i> Cassagnau.....	—	—	—	—	40	114	112	7
<i>Friezea troglaphila</i> Cassagnau.....	—	14	—	—	—	—	—	—
<i>Friezea</i> cf. <i>nevadensis</i> Steiner.....	—	—	—	—	1	9	—	—
<i>Xenyllodes armatus</i> Axelson.....	—	—	248	738	—	—	—	—
<i>Microgastrura cantabrica</i> Simón-Pozo..	—	—	—	—	3	34	—	—
<i>Brachystomella parvula</i> Schäffer.....	10	—	—	3	—	12	580	48
<i>Pseudachorutes palmiensis</i> Börner....	1	—	5	1	2	—	—	—
<i>Pratanurida fagusensis</i> nov. sp.....	1	—	—	—	—	—	—	—
<i>Micranurida meridionalis</i> Cassagnau...	3	1	—	1	—	—	—	—
<i>Micranurida pygmaea</i> Börner.....	—	—	—	—	4	—	—	—
<i>Monobella grassei</i> (Denis).....	—	—	3	—	—	—	—	—
<i>Endonura alavensis</i> Pozo-Simón.....	3	—	2	—	—	1	—	—
<i>Deutonura plena</i> Stach.....	6	3	1	1	1	1	—	—
<i>Deutonura plena trioculata</i> Pozo-Simón.	—	—	—	—	—	1	—	—
<i>Deutonura sinistra</i> (Denis).....	—	5	1	—	—	—	—	—
<i>Neanura</i> sp.....	—	—	3	3	—	—	—	—
<i>Oligaphorura serratotuberculata</i> (Stach).	—	7	—	—	—	—	—	—
<i>Kalaphorura burmeisteri</i> (Lubbock)....	1	1	—	—	—	—	—	—
<i>Protaphorura cancellata</i> Gisin.....	29	194	9	3	—	—	—	—
<i>Protaphorura armata</i> (Tullberg).....	—	8	—	—	—	—	—	—
<i>Onychiurus cavernicolus</i> Stach.....	—	15	—	—	—	—	—	—
<i>Paratullbergia callipygos</i> (Börner)....	1	250	2	201	—	13	3	51
<i>Mesaphorura</i> gr. <i>krausbaueri</i> Börner...	4	146	3	497	127	312	75	555
<i>Stenaphorura quadrispina</i> (Börner)....	—	—	—	4	—	—	—	—
<i>Anurophorus oredonensis</i> Cassagnau...	—	—	—	—	—	—	1	—
<i>Anurophorus laricis</i> Nicolet.....	—	—	—	—	1	—	—	—
<i>Folsomia candida</i> Willem.....	—	—	—	—	—	—	—	2
<i>Folsomia quadrioculata</i> (Tullberg)....	152	51	534	352	51	75	—	—
<i>Folsomia setosa</i> Gisin.....	92	36	—	—	—	—	—	—
<i>Folsomia sexoculata</i> (Tullberg).....	288	686	53	131	—	—	—	—
<i>Isotomodes productus</i> (Axelson).....	—	—	—	—	—	—	—	13
<i>Isotomiella minor</i> (Schäffer).....	83	141	6	59	37	244	—	—
<i>Vertagopus cinerea</i> (Nicolet).....	—	—	—	—	2	2	—	—
<i>Isotoma monochaeta</i> Kos.....	—	—	2	2	886	141	—	—
<i>Isotoma notabilis</i> Schäffer.....	57	18	52	73	76	59	207	226
<i>Isotoma</i> cf. <i>antennalis</i> (Bagnall).....	—	—	—	1	—	—	—	—
<i>Isotoma</i> cf. <i>maritima</i> Tullberg.....	—	—	—	—	6	—	—	—

TAB. II (Continuation)

Species	Beech Forest		Oak Forest		Pine Forest		Meadow	
	L	S	L	S	L	S	L	S
<i>Isotomurus palustris</i> (Müller).....	10	2	23	3	436	30	267	32
<i>Entomobrya</i> gr. <i>lanuginosa</i> (Nicolet)...	15	2	47	77	8	2	13	15
<i>Entomobrya marginata</i> (Tullberg).....	3	—	—	—	—	—	—	—
<i>Entomobrya nevadensis</i> Steiner.....	—	—	23	1	—	—	—	—
<i>Heteromurus major</i> (Moniez).....	22	2	24	10	4	7	5	—
<i>Lepidocyrtus cyaneus</i> Tullberg.....	1	—	—	—	—	—	33	37
<i>Lepidocyrtus</i> gr. <i>lanuginosus</i> (Gmelin).	28	5	57	11	1	9	—	—
<i>Lepidocyrtus</i> cf. <i>curvicollis</i> Bourlet.....	—	—	28	7	—	—	—	—
<i>Pseudosinella alba</i> (Packard).....	2	46	—	1	—	—	2	10
<i>Pseudosinella</i> cf. <i>decipiens</i> * Denis.....	2	5	—	—	—	—	1	29
<i>Pseudosinella tarraconensis</i> Bonet.....	—	—	—	—	—	2	—	—
<i>Pseudosinella</i> cf. <i>duodecimoculata</i> Denis.	—	—	18	3	—	—	—	—
<i>Tomocerus catalanus</i> Denis.....	—	—	—	—	1	—	—	—
<i>Tomocerus minor</i> (Lubbock).....	3	—	—	—	1	—	—	—
<i>Cyphoderus albinus</i> Nicolet.....	—	—	—	—	—	—	2	10
<i>Megalothorax minimus</i> Willem.....	—	—	—	—	—	1	—	—
<i>Sphaeridia pumilis</i> (Krausbauer).....	11	—	16	—	8	—	88	2
<i>Sminthurides alpinus</i> Cassagnau.....	—	—	—	—	16	—	—	—
<i>Sminthurides schoetti</i> Axelson.....	—	—	—	—	—	—	1	—
<i>Sminthurides</i> cf. <i>violaceus</i> (Reuter)....	3	—	—	—	—	—	—	—
<i>Arrhopalites acanthophthalmus</i> Gisin...	1	—	—	—	—	—	—	—
<i>Arrhopalites microphthalmus</i> Cassagnau-	—	—	—	—	—	—	—	—
Delamare.....	—	—	—	1	—	—	—	—
<i>Arrhopalites sericus</i> Gisin.....	5	—	—	—	—	—	—	—
<i>Sminthurinus aureus</i> (Lubbock).....	50	2	58	6	82	3	—	—
<i>Sminthurinus elegans</i> (Fitch).....	3	—	—	—	—	—	11	7
<i>Sminthurinus niger</i> (Lubbock).....	—	—	—	—	—	—	3	—
<i>Sminthurinus</i> cf. <i>denisi</i> (Cassagnau)...	—	—	—	—	—	—	9	4
<i>Sminthurinus</i> ♂♂.....	—	—	—	—	—	7	—	—
<i>Katiannidae</i> young.....	—	—	—	—	—	—	22	1
<i>Allacma fusca</i> (Linneo).....	—	—	1	1	—	—	—	—
<i>Caprainea marginata</i> (Schott).....	—	—	—	—	—	—	6	—
<i>Caprainea</i> sp.....	2	—	—	—	—	—	—	—
<i>Sminthurus</i> cf. <i>multifasciatus</i> Reuter..	—	—	—	—	—	—	—	2
<i>Lipothrix lubbocki</i> (Tullberg).....	1	—	—	1	—	—	—	—
<i>Vesicephalus europaeus</i> Ardanaz-Pozo..	1	—	—	—	—	—	—	—
<i>Dicyrtoma melitensis</i> Stach.....	—	—	1	—	—	—	—	—
<i>Sminthuridae</i> damaged.....	—	—	1	1	—	—	—	—
TOTAL.....	982	1 674	1 313	2 201	2 022	1 374	1 447	1 054

producing vertical migrations of species that look for favourable conditions of temperature and moisture (TAKEDA, 1978). Soil water content has an important influence on collembola (POOLE, 1961, 1962; USHER, 1976) and since it is a parameter affected by temperature, the fluctuations in number of collembola are often imputed to both factors (BELLINGER, 1954; NOSEK, 1981; VANNIER, 1970).

From table II it can be concluded that the area with bigger specific richness is the forest of *F. silvatica* (45 species). Oakwood and pinewood follow it with 37 and 35 species respectively. The meadow has the lowest one with 25 species. Respect this, WALLWORK (1970) has pointed out that the forest soil supports a collembological fauna more varied than the meadows. It seems that the reason is the protective effect of the vegetation cover and the existence of well developed organic layers. It can be seen that the litter of the beechwood shelters more species than its soil (40 and 26 respectively) whereas the remaining areas keep similar number of species in the superficial layer and in the soil (30 and 31, in the oakwood; 26 and 26, in the pine wood; 22 and 19, in the meadow).

As a whole, the collembola of this survey are represented by 82 species and groups of species. Each collembolan community is characterized by the dominance of a few species representing a high percentage of individuals. Only 12 species have abundances upon 5 % in some of the studied sites. These are: in the beechwood, *Folsomia sexoculata* (36.7 %), *Paratullbergia callipygos* (9.4 %), *Isotomiella minor* (8.4 %), *Protaphorura cancellata* (8.4 %), *Folsomia quadrioculata* (7.6 %) and *Mesaphorura* gr. *krausbaueri* (5.6 %); in the oakwood, *Xenyllodes armatus* (28.1 %), *F. quadrioculata* (25.2 %), *M. gr. krausbaueri* (14.2 %), *P. callipygos* (5.8 %) and *F. sexoculata* (5.2 %); in the pinewood, *Isotoma monochaeta* (30.2 %), *Isotomurus palustris* (13.7 %), *M. gr. krausbaueri* (12.9 %), *Ceratophysella armata* (11.5 %) and *I. minor* (8.3 %); in the meadow, *M. gr. krausbaueri* (25.2 %), *Brachystomella parvula* (23.9 %), *Isotoma notabilis* (17.7 %) and *I. palustris* (11.9 %). Only *M. gr. krausbaueri* develops high numbers of individuals in all the studied sites, more in the meadow. In another hand, it may be pointed out the inverted hierarchical importance of *F. sexoculata* and *F. quadrioculata* in the areas where they coexist. Thus, while *F. sexoculata* clearly dominates in the beechwood, *F. quadrioculata* does it in the oakwood. Only the latter species is present in the pine forest and both of them are absent from the meadow.

2. Diversity.

Although the diversity of a community appears as an instantaneous property, it is the result of the ecosystem operation (MARGALEF, 1969) and its calculation as a method for comparing different samples has been repeatedly used in soil biology for the last years. In the case of the collembola (BETSCH *et al.*, 1981; HAGVAR & KJØNDAL, 1981; HERMOSILLA, 1982; LIENHARD, 1980; MASSOUD *et al.*, 1984; PRAT & MASSOUD, 1981), the types of works are difficult to compare.

Results obtained by using diversity indices are shown in table III. They correspond to the actual values registered in each season.

In the beech litter, the values of the species diversity index (H) varied from 2.77 (August) to 3.45 (November). It is in summer when species richness is minimal too ($H_{max} = 3.00$) and when the greatest value of evenness is obtained ($E = 0.92$), which indicates an homogeneous distribution of individuals among the present species. Referring to soil, the greatest H value were registered in February (3.22) while the smallest did correspond to May (2.31), when *Folsomia sexoculata* represented more than 50 % of collembola, causing a decrease of evenness ($E = 0.54$).

TAB. III

Actual values of the diversity indices in both litter (L) and soil (S) of the studied sites.

H = species diversity, Hmax = maximum diversity (species richness), E = evenness

		November		February		May		August	
		L	S	L	S	L	S	L	S
Beech forest	H.....	3.45	2.51	3.28	3.22	3.11	2.31	2.77	2.81
	Hmax.....	4.86	4.00	4.46	4.17	4.46	4.25	3.00	3.91
	E.....	0.71	0.63	0.73	0.77	0.70	0.54	0.92	0.72
Oak forest	H.....	2.56	2.63	2.61	2.00	2.62	2.65	3.29	3.24
	Hmax.....	4.58	3.58	3.46	3.70	4.09	4.09	3.91	4.32
	E.....	0.56	0.73	0.76	0.54	0.64	0.65	0.84	0.75
Pine forest	H.....	3.19	2.66	2.24	2.61	1.92	2.62	2.11	3.19
	Hmax.....	4.00	3.70	3.58	4.09	4.09	3.70	2.58	3.91
	E.....	0.80	0.72	0.62	0.64	0.47	0.71	0.82	0.82
Meadow	H.....	2.77	1.91	2.54	1.46	2.05	2.53	0.51	3.31
	Hmax.....	3.91	3.32	4.00	3.58	3.00	4.00	2.00	3.81
	E.....	0.71	0.58	0.63	0.41	0.68	0.63	0.26	0.87

In the oak forest, the H index ranged from 2.56 (November) to 3.29 (August) at litter layer. It may be pointed out that in November, when the number of species is greater (Hmax = 4.58), equitability shows the smallest value (E = 0.56), due to the abundance of *Folsomia quadrioculata* (54 % of individuals) which produces a marked unevenness in the relative proportions of species. At soil layer it may be pointed out a minimal H value in February (2.00) as a consequence of the numeric importance of *Xenyllodes armatus* and *Mesaphorura* gr. *krausbaueri*, and a maximal value in August (3.24), concurring with high species richness (Hmax = 4.32). This increase in species number is mainly due to the appearance of species such as *Brachystomella parvula*, *Arrhopalites microphthalmus* and *Lipothrix lubbocki* at this time of the year, and by the vertical migration of *Ceratophysella attenuata*, *Deutonura plena* ssp. *plena*, *Isotoma monochaeta* and *Heteromurus*, which had not been registered at this layer before summer.

Litter of pine forest did show the H values between 1.92 (May) and 3.19 (November). Both extrema values did occur when the species richness were similar (4.09 and 4.00, respectively). Since the H index is a function of both species richness and the relative abundances of species, an important decrease of evenness was shown in May (E = 0.47), when *Isotoma monochaeta* represented 66 % of individuals collected in this month in the litter layer. As in the case of the oak forest, the greatest H value in the pine forest soil did happen in August. It coincided with a high value of evenness. On the

contrary, equitability were minimum in February because the great abundance of *Mesaphorura* gr. *krausbaueri*.

The smallest species diversity was registered in the herbaceous layer of the meadow ($H = 0.51$) in summer. It was due to a strong decrease of the number of species ($H_{\max} = 2.00$) and to the high relative abundance of *Brachystomella parvula* (91.8 % of the individuals) which caused the fall of evenness ($E = 0.26$) at this time. On the contrary and at the same time, soil did show a great H value which corresponded to an homogeneous population ($E = 0.87$). This fact contrasts with the unevenness of February, when the population was dominated by *Mesaphorura* gr. *krausbaueri* ($E = 0.41$).

From a general point of view, this results show that, excepting the case of oakwood, the litter layer of the different sites revealed the greatest diversity values (H) in autumn, when also a great number of species were present. Nevertheless, the soils trend were to show high values in summer. Although the litter species richness use to overcome the soil values during November, February and May, in August is a general trend to encounter greater number of species in soil. To this we will refer below.

It can be considered that the diversity value remains constant as long as the different species remain constant too. If the union of two samples modifies the diversity, this result must be interpreted as a proof of heterogeneity between them (MARGALEF, 1974). The cumulative diversity, applied in works on successions (e.g. HERMOSILLA, 1982), according to time, will show us if new species appear and if this is accompanied by variation of the species relative proportion in the different seasons.

The results of the cumulative diversity indices (H and H_{\max}) along the seasons are plotted in figure 5. It shows that the species number (H_{\max}), settled in the litter of the different sites, become practically steady in May. In the other hand, the increase of species richness in the soil go on until summer, more clearly in the oak and pine forests. This presence of new species in the soil must be understood, in most of the cases, as a vertical migration of the upper dwelling species that look for less extreme conditions at this time of the year, when the litter is dry. This fact has been also pointed out by MASSOUD *et al.* (1984) in a forest from Seine et Marne, France. With regard to the values taken by the cumulative species diversity (H), in beechwood as well as in the meadow, the stability of this index in the litter suggest that the structure of the collembological community, observed in November, does not undergo changes along the time. The relative proportions of the species keep steady. Nearly the same happens to the litter of the oakwood, although in this case the distribution of individuals among the species tends to become homogeneous progressively. In the litter of the pine forest, the values of the diversity decrease gradually. That is basically due to the numerical importance of *I. monochaeta*, which alters continuously the relative proportion of the other species.

The dynamics of the cumulative species diversity in the different soils tends to show the H_{\max} trend, that is, the gradual increase of the number of species. However, it may be pointed out the decreases observed in February in the oakwood as well as in the meadow, caused by the great abundance of *X. armatus* and *M.* gr. *krausbaueri*, respectively.

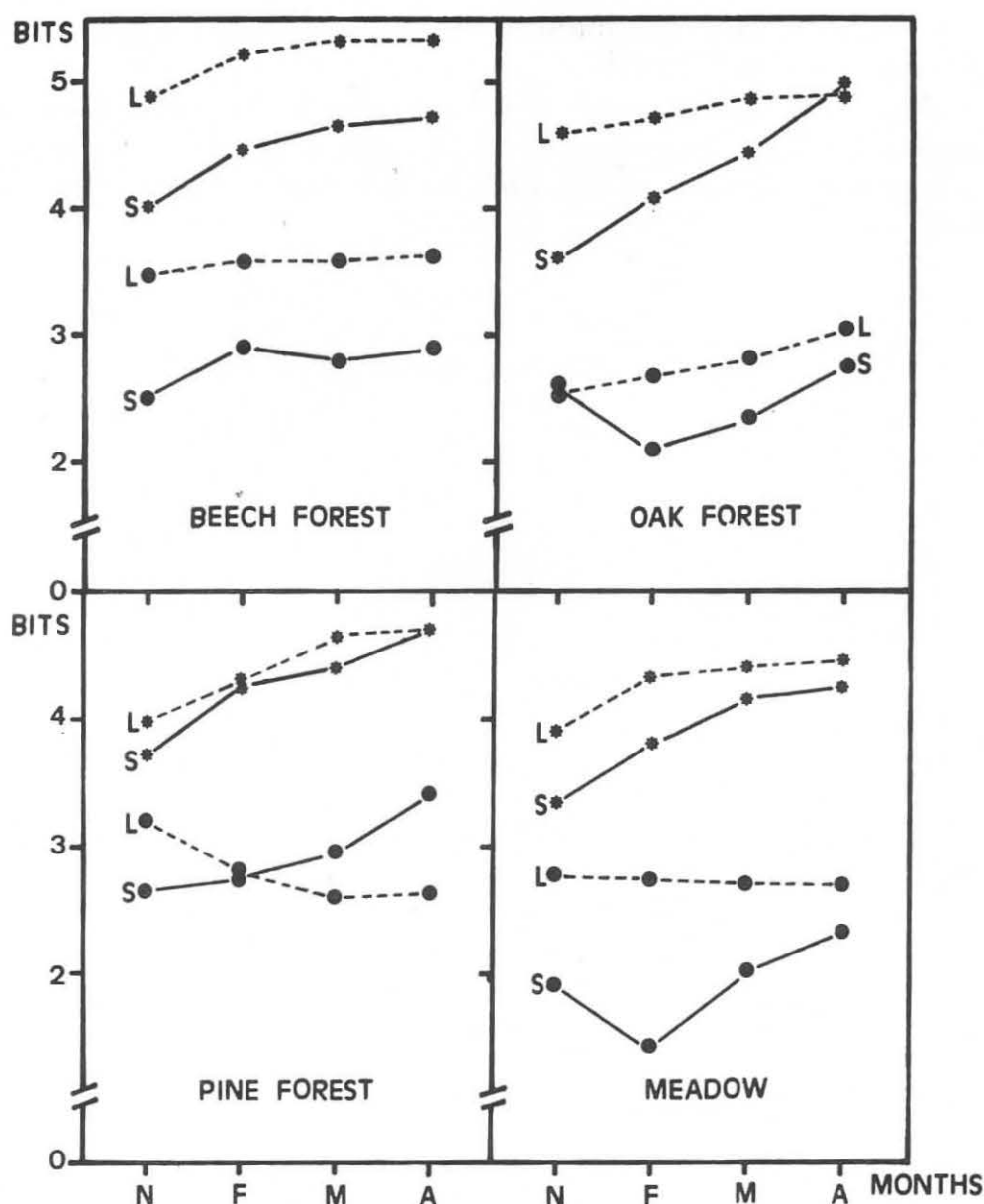


FIG. 5. — Cumulative diversity along seasons. L = Litter; S = Soil. * = Hmax; ● = H. N = November; F = February; M = May; A = August.

3. Vertical distribution of dominant species.

The vertical distribution of Collembola usually shows the largest populations in the upper centimetres of the soil profile (ASHRAF, 1971; GLASGOW, 1939; HAARLOV, 1955, 1960; HÅGVAR, 1983; HALE, 1966; NOSEK, 1981; POOLE, 1961; TAKEDA, 1978; VOLZ, 1934; WALLWORK, 1970 and others) and its position, in a particular layer, is mainly conditioned by factors such as organic matter, water content and temperature.

The sample division in two layers allows to obtain information about the presence of the fauna at different depths. Undoubtly, a mistake is made in the choice of the division plane of the layers, and usually species contaminations between them occur.

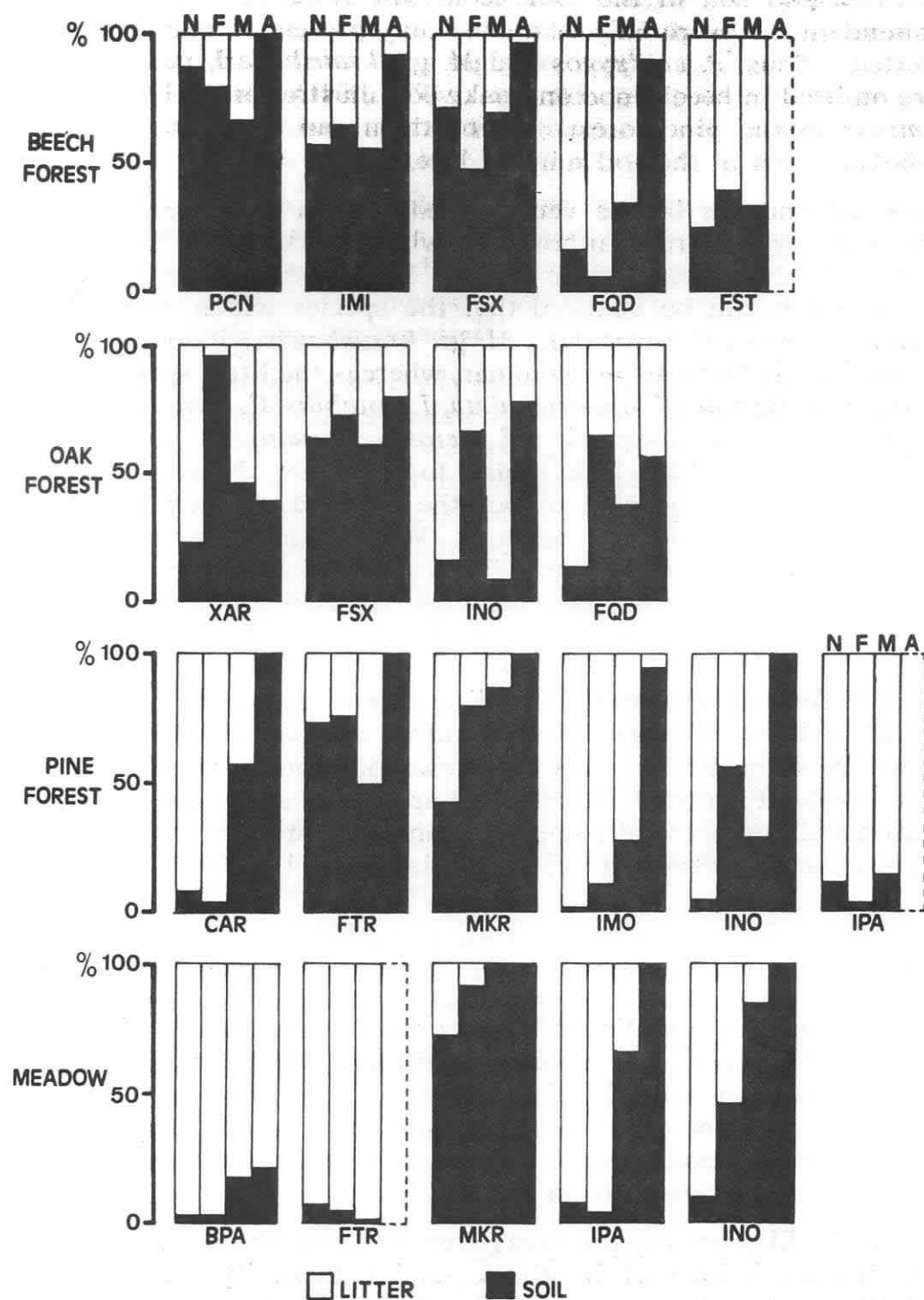


FIG. 6. — Seasonal changes in vertical distribution of the most abundant species in each area. N = November; F = February; M = May; A = August. Species code: PCN = *P. cancellata*; IMI = *I. minor*; FSX = *F. sexoculata*; FQD = *F. quadrioculata*; FST = *F. setosa*; XAR = *X. armatus*; INO = *I. notabilis*; CAR = *C. armata*; FTR = *F. truncata*; MKR = *M. gr. kraus-baueri*; IMO = *I. monochaeta*; IPA = *I. palustris*; BPA = *parvula*.

Figure 6 shows the relative proportions of the most abundant species in the litter and soil in the four ecological systems. Those species which were abundant but were only or almost only present in one of the layers are not plotted. Thus, *P. callipygos* and *M. gr. krausbaueri*, nearly restricted to soil, are omitted in beechwood and oakwood illustrations. The same happens to *I. minor* in the pine forest. All of them can be considered as specific collembolan fauna of the soil mineral layer.

Seasonal changes in the vertical distribution of Collembola have been pointed out by several authors anywhere (HÅGVAR, 1983; HALE, 1966; MACFADYEN, 1952; TAKEDA, 1978; USHER, 1970; VOLZ, 1934; WOLTERS, 1983). From figure 6 it can be deduced that the species which prevail in soil (*P. cancellata*, *I. minor*, *F. sexoculata*, *M. gr. krausbaueri*) increase their relative proportion in this layer during summer, whereas the litter species, in summer, either move to the soil (*F. quadrioculata*, *I. notabilis*, *C. armata*, *I. monochaeta* and *I. palustris*) or disappear (*F. setosa*, *I. palustris* and *F. truncata*). Obviously, this behaviour is a reply to the litter dryness in this season. Besides that, it must be pointed out the inverted position that *F. truncata* occupies in the pinewood and meadow. Whereas in the pinewood it appears mainly in the soil, in the meadow it prevails as an upper dwelling species. This fact could be explained by the organic matter content of the habitat. In the pine forest soil, it is accumulated more organic matter than in the meadow, where there is not a definite organic layer. PONGE (1980) has observed, in the region of Paris, that *F. truncata* inhabits organic matter accumulations in different types of soils and at different depths. It seems that the niche may change not only along seasons, but also along type of soil (HÅGVAR, 1983). Finally, *B. parvula* is a species that has not showed substantial seasonal differences between litter and soil and it remains as a typical species of meadow, settled in the superficial layer.

C) Synthesis.

Since a relative climatic uniformity among the studied sites exists, the climatic factors do not seem to be responsible of the differences about neither specific composition nor global densities of the collembolan populations. The feature of this factors only can be seen, in a general way, by their incidence on the populations density decreases in summer-time, especially in the superficial layers by desiccation.

The variability among the areas should be attributed mainly to edaphic factors, directly influenced by the vegetal community type and geological substratum. Thus, all the sites can be distinguishable on the basis of parameters such as organic matter content, C/N ratios and pH. There where a greater organic matter content exists (pine forest soil), it is obtained a greater C/N ratio due to a low decomposition speed; Nevertheless, this is not attended with low pH values, which are mitigated by the limestone component of the substratum. In the other cases, where the organic matter content is lower, the differentiation among the areas is due either to high C/N ratios (oak forest soil) or to the pH values (beech forest soil is the most acid, while meadow soil is the less one).

In these distinct conditions, different collembolan populations occur that differ in global densities as well as in specific composition and hierarchical structure. Thus, the most numerous populations have corresponded to the biotopes where high C/N ratios were registered (pine and oak forests) and we suppose, after WALLWORK (1970, 1976), that this must be related to the soil fertility, in the sense of showing greater abundances of collembola in soils with a low decomposition speed (high C/N ratios).

From another point of view, the basis of the hierarchy of communities corresponds to different species in each case: *Folsomia sexoculata*, in the beechwood; *Xenyllodes armatus* and *Folsomia quadrioculata*, in the oakwood; *Isotoma monochaeta*, in the pinewood; *Mesaphorura* gr. *krausbaueri* and *Brachystomella parvula*, in the meadow.

Although the actual species diversity have shown changes along the seasons, a general fact is the high values registered in fall. Moreover, looking to the results of the cumulative diversity, we can say that the hierarchical structure revealed in November does not suffer great changes along the time, although new species appear in successive seasons. The changes in diversity must be attributed, in a great extent, to the changes of abundance of the main species.

The appearance of species along the time shows different trends between the two layers studied and thus, while the species number of the litters tends to become steady in spring, the soils show a progressive increase in species richness until summer, produced by the vertical migrations of species that escape from the litter drying. This shows that the vertical distribution of collembola changes along the time, and if we consider the main species represented in figure 6, these changes are also produced among different sites. We can assume that in different types of soils the species tend to look for their ecological requirements and these can be located at different levels of the soil profile (BELLINGER, 1954; HÅGVAR, 1983).

The type of plant community shows to be of great importance too, and when there is not a vegetal cover and no well defined litter layer exists, as in the meadow, according to WALLWORK (1970), a poor number of species is expected.

SUMMARY

The structure and composition of collembolan fauna, in four different plant communities (beechwood, oakwood, pine forest and meadow) of The Basque Country (Spain), has been studied.

Some climatic and edaphic factors, that seem to affect the collembolan populations, were measured. A relationship between total abundances and C/N ratios of the soils is suggested.

The more relevant species of the communities are *Ceratophysella armata*, *Xenyllodes armatus*, *Brachystomella parvula*, *Protaphorura cancellata*, *Paratubergia callipygos*, *Mesaphorura* gr. *krausbaueri*, *Folsomia quadrioculata*, *Folsomia sexoculata*, *Isotomiella minor*, *Isotoma monochaeta*, *Isotoma notabilis* and *Isotomurus palustris*.

Seasonal changes in diversity and vertical distribution of Collembola have been detected. Results show that the number of litter species become everywhere practically steady in spring. In another hand, the increase of the number of species in soil go on until summer. At this time of the year, it can be considered, in most of the cases, as a consequence of vertical migrations of species caused by litter layer dryness.

RESUMEN

Estudios sobre las poblaciones de Colémbolos de varias comunidades vegetales del País Vasco (España)

Se ha estudiado la estructura y composición de las poblaciones de colémbolos de cuatro comunidades vegetales (hayedo, robledal, pinar y prado) del País Vasco (España).

Se han medido varios factores climáticos y edáficos que parecen afectar a las poblaciones de colémbolos. Parece existir una relación entre la abundancia de colémbolos y la relación C/N de los diferentes suelos.

Las especies más relevantes de las comunidades son *Ceratophysella armata*, *Xenyllodes armatus*, *Brachystomella parvula*, *Protaphorura cancellata*, *Paratullbergia callipygos*, *Mesaphorura* gr. *krausbaueri*, *Folsomia quadrioculata*, *Folsomia sexoculata*, *Isotomiella minor*, *Isotoma monochaeta*, *Isotoma notabilis* e *Isotomurus palustris*.

Los resultados de los cambios estacionales en la diversidad y distribución vertical de los colémbolos han puesto de manifiesto que el número de especies que habitan la hojarasca se estabiliza en la primavera, mientras que en el suelo, siguen apareciendo especies, no registradas en estaciones anteriores, hasta el verano. En esta época del año, se puede considerar que ello es debido, en la mayoría de los casos, a una migración vertical de las especies, como consecuencia de la desecación del horizonte de hojarasca.

RÉSUMÉ

Études sur les peuplements de Collemboles dans quelques communautés végétales du Pays Basque (Espagne)

On a étudié la structure et la composition des peuplements de Collemboles dans quatre communautés végétales (forêt de hêtres, forêt de chênes, forêt de pins et prairie) du Pays Basque (Espagne).

Ont été mesurés quelques facteurs climatologiques et édaphiques qui affectent les peuplements de Collemboles. Il semble exister une relation entre l'abondance des Collemboles et le rapport C/N des différents sols.

Les espèces les plus importantes des communautés sont *C. armata*, *X. armatus*, *B. parvula*, *P. cancellata*, *P. callipygos*, *M. gr. krausbaueri*, *F. quadrioculata*, *F. sexoculata*, *I. minor*, *I. monochaeta*, *I. notabilis* and *I. palustris*.

Les résultats des changements saisonniers en diversité et en distribution verticale des Collemboles ont montré d'une part, qu'il y a une stabilité du nombre des espèces qui habitent les litières dès le printemps et, d'autre part, que dans les sols, la récolte des espèces qui n'avaient pas été enregistrées dans les saisons précédentes se poursuit jusqu'à l'été. On peut considérer que ceci est dû, dans presque tous les cas, à une migration verticale des espèces, comme conséquence de la sécheresse de la litière.

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